

THE MARINE CROCODILE *MALEDICTOSUCHUS* (THALATTOSUCHIA, METRIORHYNCHIDAE) FROM THE KIMMERIDGIAN DEPOSITS OF TLAXIACO, OAXACA, SOUTHERN MEXICO

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ABSTRACT—Metriorhynchidae is a family of highly specialized, extinct marine crocodylomorphs that inhabited the Paleopacific Ocean and the Tethys Sea during the Jurassic and the Early Cretaceous. Numerous metriorhynchid fossil specimens have been recovered from European and South American localities, but North American records of this family are still scarce. Here, we describe a recently recovered Kimmeridgian metriorhynchid from the Sabinal Formation, Tlaxiaco Basin, Oaxaca, Mexico, that is attributable to the genus *Maledictosuchus*. This genus was known previously from a single species, *M. riclaensis*, from the Middle Jurassic of Spain. The characteristics of this Mexican specimen support its identification as a new species, *Maledictosuchus nuyivijanan*, sp. nov. The two species differ in dental and skull-roof morphology. The frontal of *M. nuyivijanan*, sp. nov., has a wide, rounded anterior end that extends rostrally to the same level of the anterior end of the prefrontal, whereas the frontal of *M. riclaensis* has a narrow anterior end that is located posterior to the anterior end of the prefrontal. Additionally, the teeth of *M. nuyivijanan*, sp. nov., exhibit bicarinated crowns, a smooth labial surface, and a lingual surface ornamented with longitudinal ridges, whereas those of *M. riclaensis* lack carinae and the labial and lingual surfaces are covered with considerably more conspicuous ridges. The North American occurrence of *M. nuyivijanan*, sp. nov., suggests a wider temporal and geographic distribution for the genus *Maledictosuchus* across the Tethys Sea than previously thought: from the Callovian in Europe to the Kimmeridgian in southern North America.

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SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

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INTRODUCTION

Metriorhynchidae is an extinct family of Mesozoic thalattosuchian crocodylomorphs with pelagic habits. Their adaptations to a strictly pelagic marine lifestyle include a set of highly specialized features, such as the presence of paddle-like forelimbs, a hypocercal tail, osteoporotic-like bone tissue, and large and highly vascularized nasal salt glands draining toward the preorbital fossa, as well as the reduction of the olfactory tract and bulbs (Fernández and Gasparini, 2008; Fernández and Herrera, 2009; Young et al., 2010; Herrera et al., 2013a, 2013b). Fossils of metriorhynchids have been collected in Europe (e.g., England, France, Spain) and the Americas (Mexico, Cuba, Argentina, Chile) (Andrews, 1913; Young, 1948; Gasparini and Chong-Díaz, 1977; Gasparini and Iturralde-Vinent, 2006; Buchy et al., 2007; Wilkinson et al., 2008; Herrera et al., 2015; Barrientos-Lara et al., 2016).

Currently, the 30–40 known metriorhynchid species are grouped in two subfamilies, Metriorhynchinae and

Geosaurinae, and approximately 14 genera (Young et al., 2013a, 2013b). Among metriorhynchines, the tribe Rhacheosaurini, a group of species that are inferred to have hunted small and agile prey, is distinguished by having elongated skulls ending in tubular snouts armed with small conical teeth, usually with non-serrated carinae (Pol and Gasparini, 2009; Young et al., 2011; Parrilla-Bel et al., 2013). Currently, this tribe includes approximately nine species among *Cricosaurus* Wagner, 1852, *Rhacheosaurus gracilis* von Meyer, 1831, and *Maledictosuchus riclaensis* Parrilla-Bel, Young, Moreno-Azanza, and Canudo, 2013.

Several Mexican metriorhynchid specimens have been collected from Jurassic marine deposits in the center and north of Mexico. These comprise *Torvoneustes mexicanus* (Wieland, 1910), from an uncertain locality near Tlaxiaco town, Oaxaca (Barrientos-Lara et al., 2016); *Cricosaurus saltillensis* Buchy, Vignaud, Frey, Stinnesbeck, and González, 2006, from Sierra de Buñuelas, near Gómez Farías, Coahuila; *Cricosaurus vignaudi* Frey, Buchy, Stinnesbeck, and López-Oliva, 2002, from the middle Tithonian deposits of the La Pimienta Formation, near

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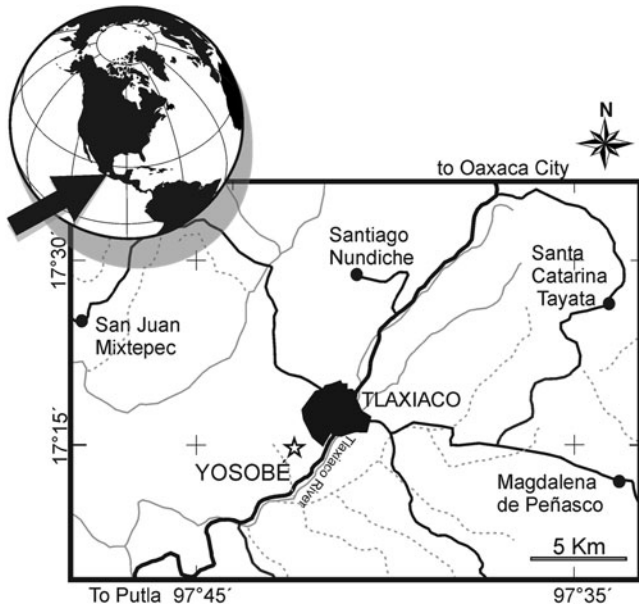


FIGURE 1. Map of the Llano Yosobé locality, near Tlaxiaco, Oaxaca, Mexico.

Mazatepec, Puebla; a fragmentary rostrum of *Dakosaurus* Quenstedt, 1856, from Kimmeridgian deposits of the La Casita Formation, near San Juan de los Dolores, Coahuila (Buchy, 2008); and some unidentified remains from the La Casita and La Caja formations, in Coahuila and Nuevo León (Buchy, 2007). Notably, during the last decade, an increasing number of metriorhynchid remains have been recovered from Llano Yosobé (Fig. 1), a site exposing marine deposits of Kimmeridgian age of the Sabinal Formation, near Tlaxiaco, Oaxaca, southern Mexico (Alvarado-Ortega et al., 2014).

The Sabinal Formation is a Kimmeridgian–Tithonian marine sedimentary unit in the Tlaxiaco Basin that consists of a sequence of clayey marls intercalated with 5–20-cm thin, layered strata of dark gray to black bituminous shale and limestone, in which abundant concretions occur (Meneses-Rocha et al., 1994). The rich fossil assemblage recovered from Llano Yosobé includes marine fishes and reptiles, ammonites, bivalves, and carbonized wood fragments, most of which have been recovered from within marl nodules (Gutiérrez-Zamora, 2011; Alvarado-Ortega et al., 2014; Barrientos-Lara et al., 2016; Barrientos-Lara, 2016; Alvarado-Ortega and Brito, 2016; López-Conde et al., 2017; Brito et al., 2017).

The aim of this paper is to describe the first Mexican specimen of *Maledictosuchus*, found at the Llano Yosobé locality, and to determine its phylogenetic relationships within the family Metriorhynchidae.

Institutional Abbreviations—**IGM**, Colección Nacional de Paleontología, Instituto de Geología, UNAM, Mexico City, Mexico; **MACN**, Museo Argentino de Ciencias Naturales Buenos Aires, Argentina; **MJCM**, Museo de Ciencias Naturales y Antropológicas ‘Juan Cornelio Moyan,’ Mendoza, Argentina; **MLP**, Museo de La Plata, La Plata, Argentina; **MOZ**, Museo Provincial de Ciencias Naturales ‘Prof. Dr. Juan Augusto Olsacher,’ Zapala, Neuquén, Argentina; **MUDE**, Museo del Desierto, Saltillo, Coahuila, Mexico; **UANL FCT**, Facultad de Ciencias de la Tierra, Universidad Autónoma de Nuevo León, Campus Linares, Mexico.

MATERIALS AND METHODS

The specimen of *Maledictosuchus* studied here was found within a nodule. It was extracted from the nodule mechanically, using an air-powered micro-chisel tool, and the bones were hardened with a light Plexigum solution. To enhance our observations, the specimen was coated with ammonium chloride and magnesium smoke. An isolated tooth was coated with gold to allow it to be studied under the scanning electron microscope (SEM), to assess the patterns of the enamel ornaments along the carinae and crown surfaces.

Anatomical Abbreviations—The morphological nomenclature and abbreviations used in this work are based on those used in other descriptions of metriorhynchids (e.g., Andrews, 1913; Fernández and Gasparini, 2000; Buchy et al., 2006, 2013; Andrade et al., 2010; Young et al., 2010, 2011, 2012, 2013a, 2013b, 2013c; Herrera et al., 2013a, 2013b, 2013c, 2015; Parrilla-Bel et al., 2013).

Comparative Materials—The following specimens were examined in this work for comparative purposes. *Cricosaurus araucanensis* (Gasparini and Dellapé, 1976): MLP 72-IV-7-1 (holotype), complete skull and postcranial skeleton; MACN N 64, anterior skull fragment; MACN N 95, complete skull and cervical vertebrae. *Cricosaurus lithographicus* Herrera, Fernández, and Gasparini, 2013c: MOZ-PV-5787 (holotype), complete skull, jaws, and some postcranial elements. *Cricosaurus saltillensis*: MUDE CPC 218 (holotype), posterior skull fragment, jaws, and cervical centra. *Cricosaurus vignaudi*: cast of UANL FCT-R1 (holotype), skull, jaws, and cervical centra. *Dakosaurus andinensis* Vignaud and Gasparini, 1996: MOZ- 6146 (holotype), skull and jaws. *Dakosaurus* sp.: MUDE CPC 201, rostral fragment reported by Buchy et al. (2007). *Purranisaurus potens* Rusconi, 1948: MJCM PV 2060 (holotype), posterior part of the skull and fragment of the right jaw.

Phylogenetic Analysis—The relationships of the new species described here were explored using a phylogenetic analysis of the family Metriorhynchidae. This analysis was performed using a data matrix that we modified from previous studies (Young et al., 2012; Parrilla-Bel et al., 2013; Herrera et al., 2015), which consists of 77 taxa and 240 characters (see [Supplementary Data 1](#) and 2). The matrix was analyzed in TNT 1.1 (Goloboff et al., 2008), using the sectorial search, tree fusion, and ratchet and drift search strategies. As in previous studies, *Postosuchus kirkpatricki* Chatterjee, 1985, was used as the outgroup (see Herrera et al., 2015). The search parameters were modified as follows: 100 sectorial search drifting cycles, 100 ratchet iterations, 100 drift cycles, and 100 rounds of tree fusion per replicate. The tree-space search procedure was run five times with different random start seeds. Bremer and bootstrap supports (1000 replicates) were calculated to assess the statistical support for the results.

SYSTEMATIC PALEONTOLOGY

Superorder CROCODYLOMORPHA Hay, 1930 (sensu Walker, 1970)

Infraorder THALATTOSUCHIA Fraas, 1901 (sensu Young and Andrade, 2009)

Family METRIORHYNCHIDAE Fitzinger, 1843

Subfamily METRIORHYNCHINAE Fitzinger, 1843

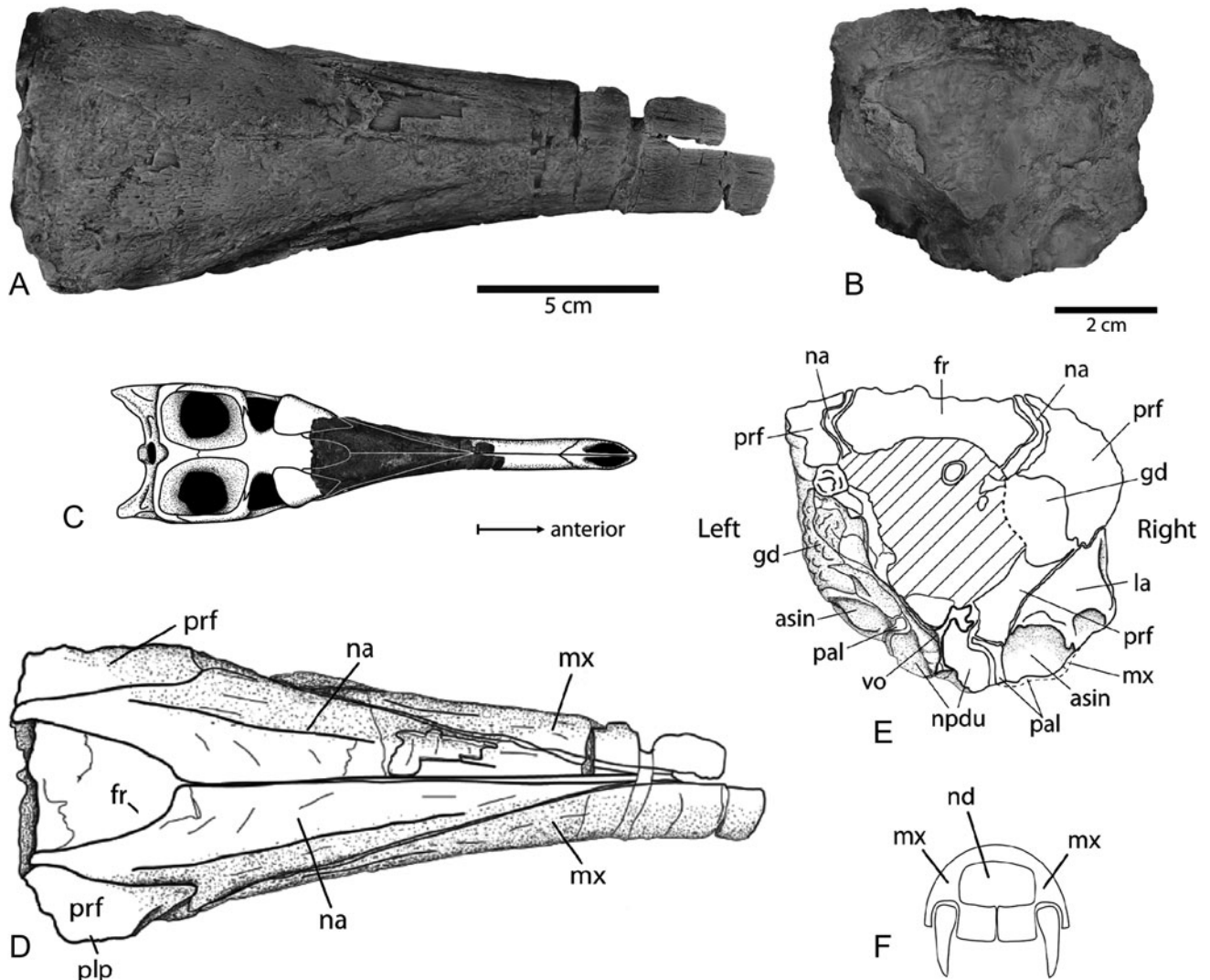


FIGURE 2. *Maledictosuchus nuyivijanan*, sp. nov., IGM 4863, rostrum fragment. **A**, dorsal view; **B**, posterior view; **C**, line drawing of the dorsal view; **D**, line drawing of the posterior view; **E**, line drawing of the posterior view; **F**, idealized line drawing in cross-section of the anterior end of the snout of this specimen. **Abbreviations:** asin, antorbital sinus; fr, frontal; gd, nasal salt gland; la, lacrimal; mx, maxilla; na, nasal; nd, nasal duct; npdu, nasopharyngeal duct; pal, palatine; plp, prefrontal lateral process; prf, prefrontal; vo, vomer.

Tribe RHACHEOSAURINI Young, Bell, and Brusatte, 2011

Genus MALEDICTOSUCHUS Parrilla-Bel, Young, Moreno-Azanza, and Canudo, 201358

Included Species—Heretofore, *Maledictosuchus* was considered a monospecific genus, represented only by *M. riclaensis* from the middle Callovian marine deposits of the Ágrede Formation at the Barranco de la Paridera site, Municipality of Ricla, Zaragoza, Spain (Parrilla-Bel et al., 2013; Parrilla-Bel and Canudo, 2015).

Emended Diagnosis—Species within the tribe Rhacheosaurini with the following unique combination of characters (autapomorphic characters identified by Parrilla-Bel et al. [2013] are indicated by asterisks; newly identified autapomorphies are indicated by double asterisks): narrow skull with a

mesorostrine snout (snout contributes 69% of basicranial length); thin lacrimal anterior process that forms a contact with the maxilla and excludes the jugal from the preorbital fenestra*; orbits longer than supratemporal fenestrae*; supratemporal fossae subsquare/subcircular, with subequal anteroposterior and lateromedial axes; lateral and medial processes of the frontal form an angle of approximately 60°; rounded rostromedial border of the supratemporal fossa (intratemporal flange); frontal ornamented with shallow radial grooves; in dorsal view, the minimum width of the frontal between the orbits subequal to the width of the supratemporal fossa; palatines with three anterior processes, one middle and two lateral processes, forming a ‘W’-shaped suture with the maxillae; anterior margin of the choanae ‘W’-shaped, with its base directed anteriorly; basi-sphenoid with paired ridges located medially on the ventral surface; heterodont dentition, including anterior maxillary teeth moderately-to-strongly mediolaterally compressed and posterior maxillary teeth subcircular in cross-section; tooth crowns bicarinated or uncarinated**; enamel on labial and

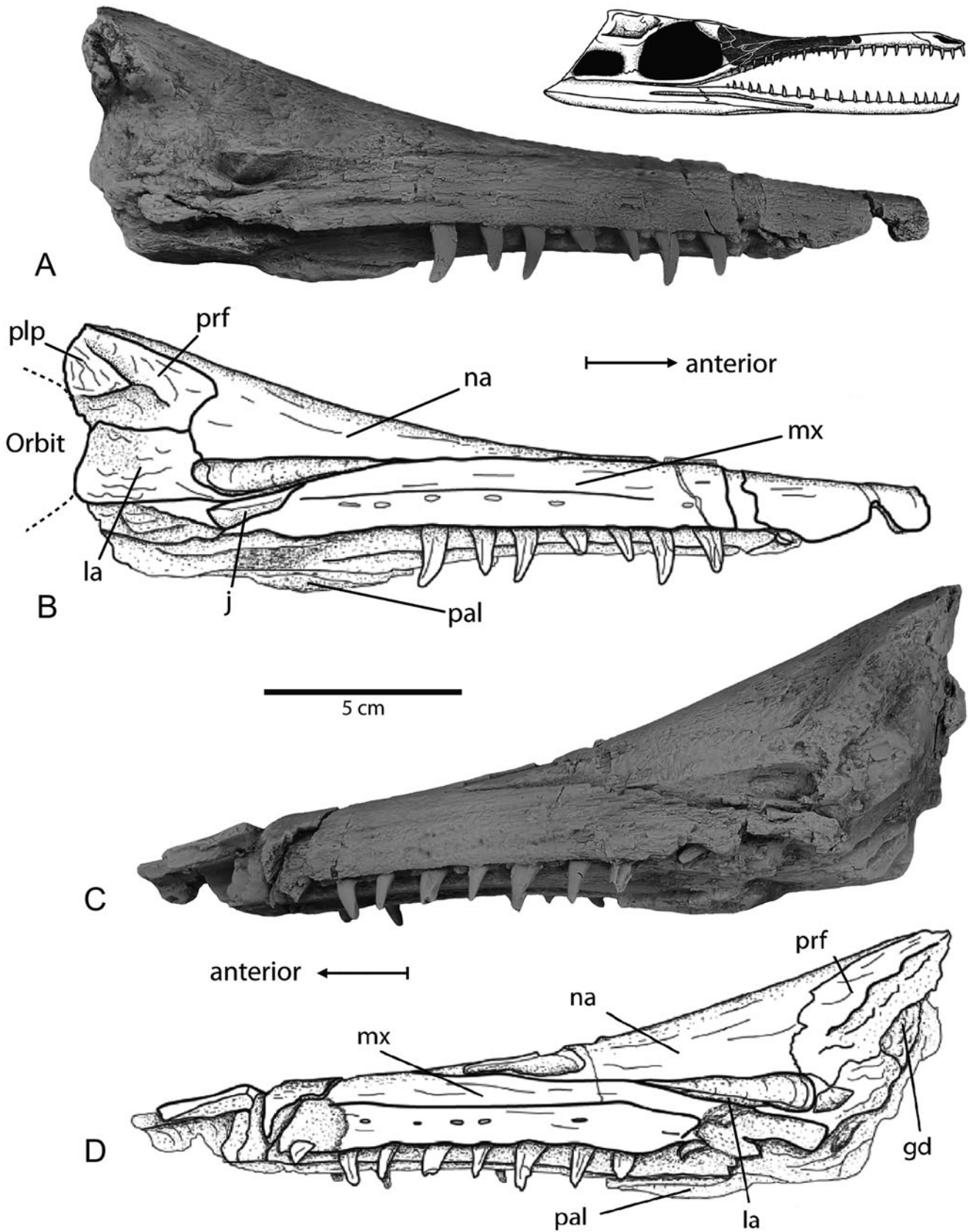


FIGURE 3. *Maledictosuchus nuyivijanan*, sp. nov., IGM 4863, rostrum fragment. **A**, right lateral view; **B**, line drawing of the right lateral view; **C**, left lateral view; **D**, line drawing of the left lateral view. **Abbreviations:** **gd**, nasal salt gland; **j**, jugal; **la**, lacrimal; **mx**, maxilla; **na**, nasal; **pal**, palatine; **plp**, prefrontal lateral process; **prf**, prefrontal.

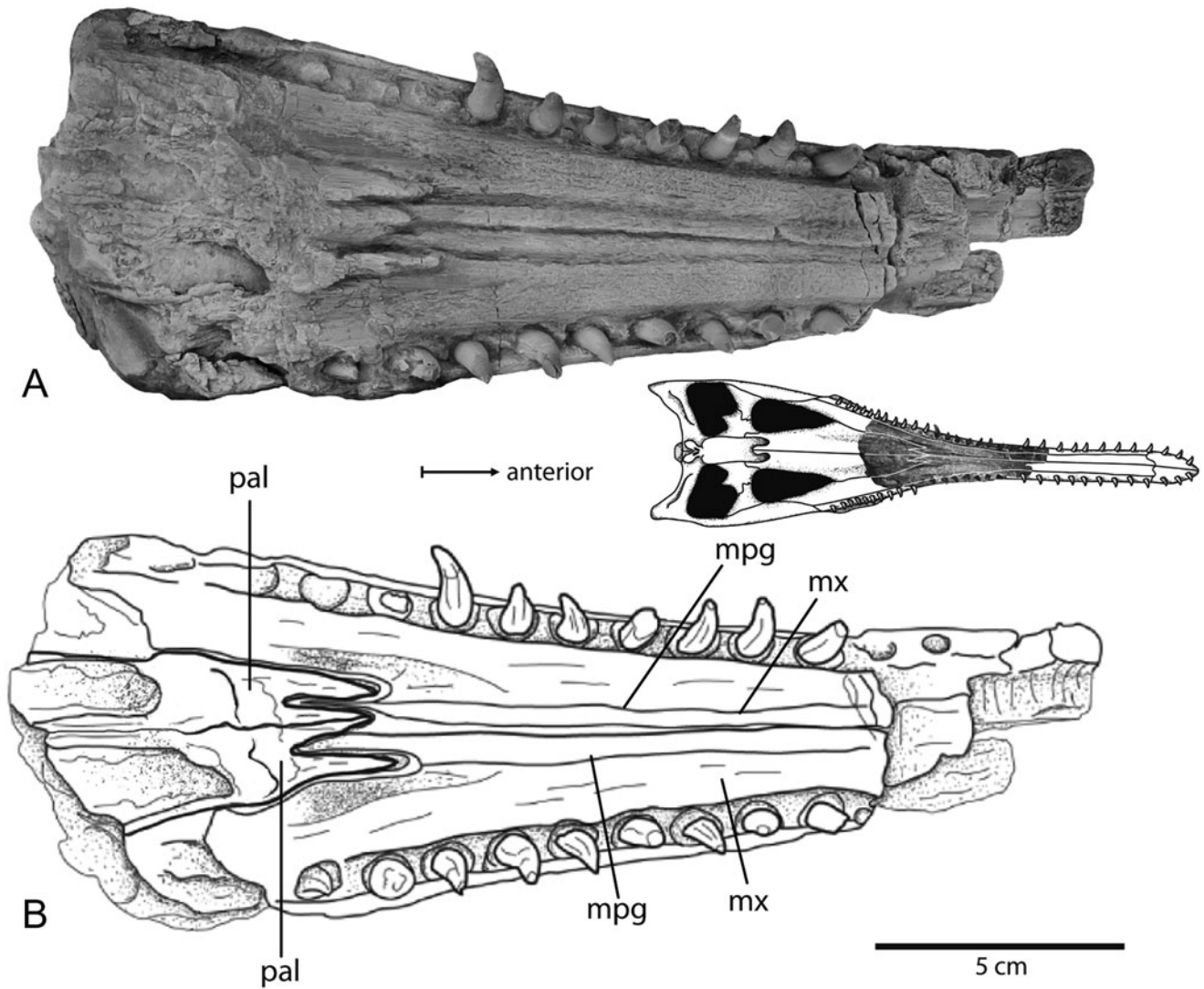


FIGURE 4. *Maledictosuchus nuyivijanan*, sp. nov., IGM 4863, rostrum fragment. **A**, ventral view; **B**, line drawing of the ventral view. **Abbreviations:** **mpg**, maxillopalatine grooves; **mx**, maxilla; **pal**, palatine.

lingual surfaces of the crowns, or only on the labial surfaces, ornamented with apicobasal accessory ridges**; maxillae with 30–33 teeth, of which approximately 18 are located anterior to the palatines; dentary with 20–21 teeth adjacent to the mandibular symphysis; and reception pits between the maxillary alveoli, offset slightly laterally on the anterior region of the maxillae and medially on the posterior region of the maxillae, caused by the dentary crowns and reception pits between dentary alveoli, caused by the maxillary crowns*.

MALEDICTOSUCHUS NUYIVIJANAN, sp. nov.

Holotype—IGM 4863, rostral fragment, 200 mm in length (Figs. 2–5).

Etymology—The specific epithet derives from two words in Mixtec, a prehispanic language that is still spoken by the local people of Tlaxiaco; ‘ñuyivi’ and ‘janaán,’ which mean ‘world’ and ‘ancient,’ respectively. The combination of both the generic name and the specific epithet means ‘the damned crocodile of the ancient world.’

Locality and Horizon—Llano Yosobé, near Tlaxiaco, Oaxaca, Mexico, a marine deposit of Kimmeridgian age within the Sabinal Formation (Fig. 1).

Diagnosis—This species differs from the type species of the genus in the following unique combination of characters: anterior end of the frontal bone comparatively wider, longer, and laterally expanded, forming a rounded stout anterior process that extends anteriorly, reaching the anterior borders of the prefrontal bones; and teeth bicarinated and ornamented with apicobasal discontinuous ridges on the basal two-thirds of the labial surfaces of the crowns.

Description

General Aspects—IGM 4863 preserves part of the external rostrum, which includes the area of the suture between the maxillae and palatines and the surface of contact between the nasal, frontal, and prefrontal bones (Figs. 2–5). The overall shape of the rostrum can be described as half of a truncated cone. This fossil is posteriorly broad at the posterior ends and

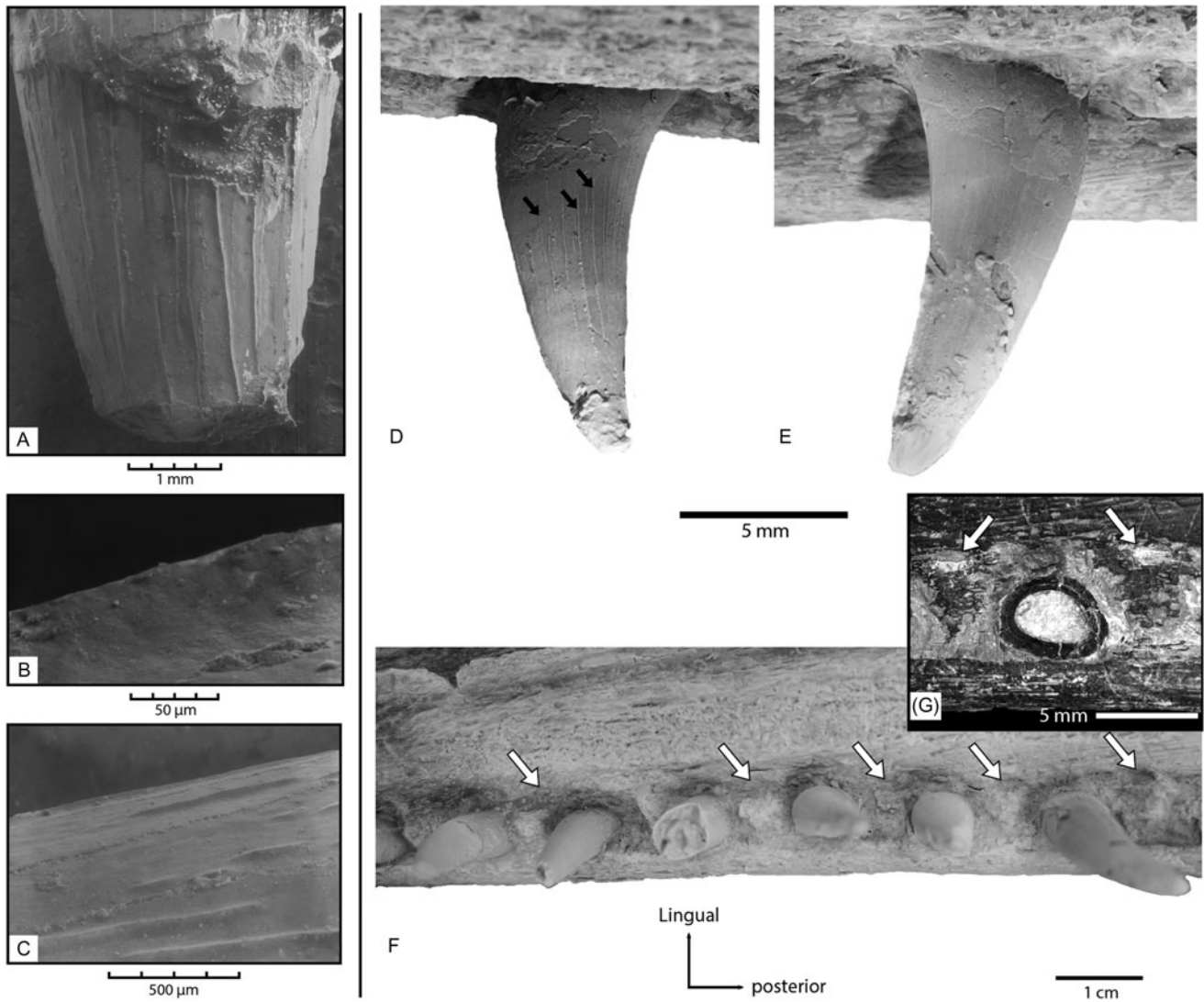


FIGURE 5. *Maledictosuchus nuyivijanan*, sp. nov., IGM 4863, details of the alveoli and dental ornamentation. **A**, (SEM) photograph of an isolated tooth in lingual view; **B**, SEM photograph of lingual view of the tooth mesial carina; **C**, SEM photograph of the ornamentation of the tooth lingual surface; **D**, lingual view of the fifth maxillary tooth; **E**, labial view of the fifth maxillary tooth; **F**, teeth of the right maxilla (the white arrows show the reception pits); **G**, close-up of the maxillary alveolus. In **D**, the black arrows show longitudinal ridges on the crown surface; in **F** and **G**, the white arrows show the reception pits.

decreases in transverse width towards the anterior end, its ventral or palatal surface is nearly flat, and its dorsal and lateral surfaces are smoothly curved. In dorsal view, the lateral edges of the specimen are slightly concave. All bones are tightly attached to one another. They are weakly ornamented with an irregular pattern of ridges and anastomosing grooves. A row of teeth is present on the lateral edge of both sides of the rostrum.

Both anterior and posterior edges of IGM 4863 show cross-sections of the skull (Fig. 2F). In the anterior cross-section, the thick maxillae constitute both halves of the semicircular cross-section. The dorsolateral surface is smoothly curved, and the ventral surface is relatively flat but with a central ridge laterally flanked by shallow tooth grooves. A single wide nasal cavity with a trapezoidal outline pierces the center of this cross-section.

The posterior cross-section of the skull exposes fragments of different bones, including the frontal, prefrontals, lacrimals, maxillae, palatines, and vomers (Fig. 2B, E). In this cross-

section, both antorbital sinuses are exposed, each of them surrounded by the palatine ventrally, the maxilla laterally, and the lacrimal dorsally. The nasopharyngeal ducts are surrounded by the palatine and the vomer. The external molds of both nasal salt glands are partially visible in this cross-section. These molds are located near, above, and behind the preorbital fossa on both sides of the skull, being surrounded by the prefrontal, the nasal, and the lacrimal, close to the suture between the nasal and the prefrontal. A large part of the external cast of the left nasal salt gland is well exposed, kidney-shaped, and with a surface with the typical lobular or blackberry-like appearance already described in other metriorhynchids (Fernández and Gasparini, 2000, 2008; Fernández and Herrera, 2009), including the type species of *Maledictosuchus* (Parrilla-Bell et al., 2016).

Frontal—The anterior end of the frontal is preserved as a thick and transversally expanded triangular bone located along the midline of the skull, between the posteromedial processes

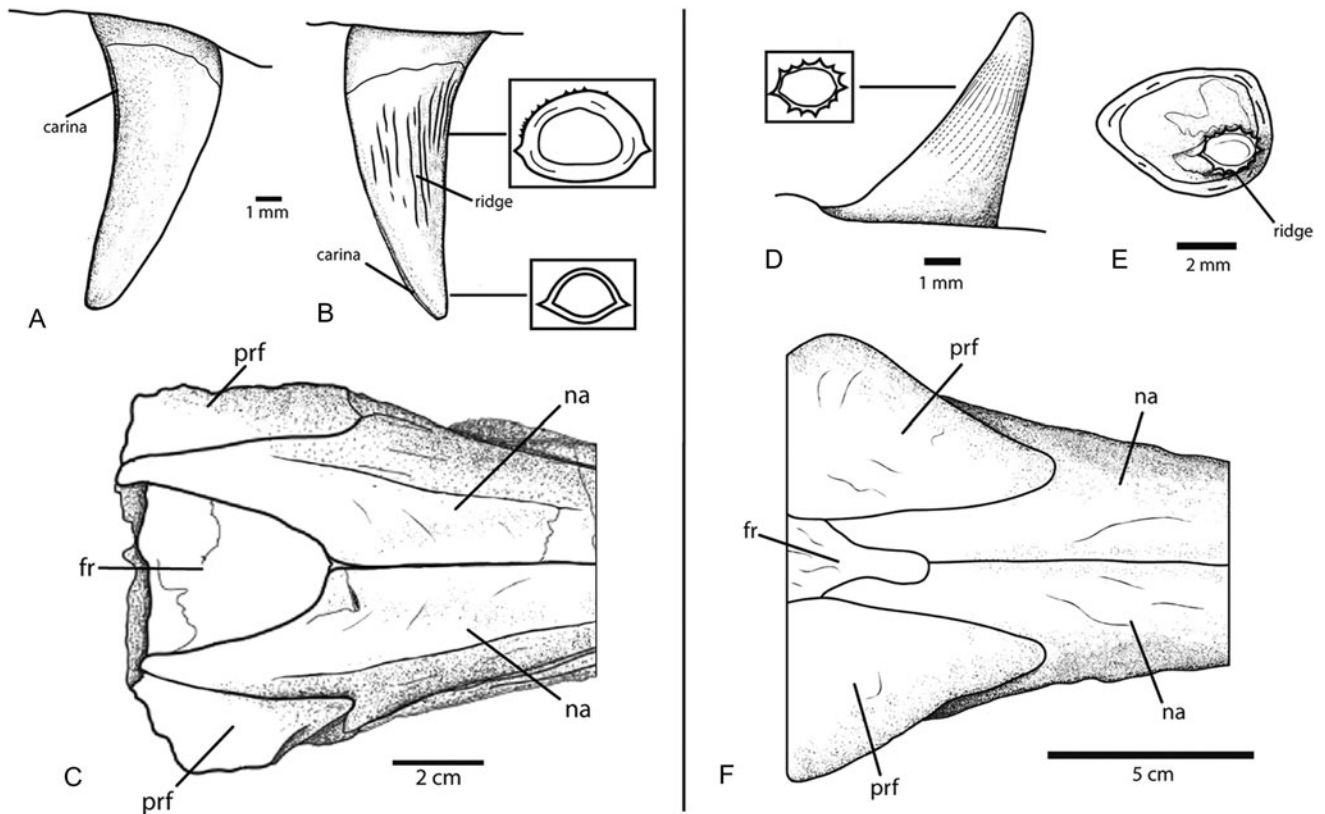


FIGURE 6. Comparative drawings of tooth and rostrum characters between *Maledictosuchus nuyivijanan*, sp. nov. (A–C) and *Maledictosuchus riclaensis* (D–F). **A**, labial surface of fifth maxillary tooth in *M. nuyivijanan*; **B**, lingual surface and cross-sections of the tooth base and apex of fifth maxilla tooth in *M. nuyivijanan*; **C**, dorsal view of the rostrum showing the anterior process of the frontal in *M. nuyivijanan*; **D**, representative tooth of *M. riclaensis* showing its superficial ornamentation and cross-section; **E**, close-up of eighth replacement tooth in *M. riclaensis*; **F**, dorsal view of the rostrum showing the anterior process of frontal in *M. riclaensis*. **D–F** based on Parilla-Bel et al., 2013:figs. 10, 15. **Abbreviations:** **fr**, frontal; **na**, nasal; **prf**, prefrontal.

of the nasals. The edges of this bone are rounded, and its dorsal surface is flat. The wide and rounded anterior process of the frontal extends anteriorly as far as the anterior ends of the prefrontal bones (Fig. 2).

Prefrontal—Only the anterior ends of the prefrontals are preserved (Figs. 2, 3). These bones are exposed on the dorso-lateral surface of the specimen, where they extend anteriorly as far as the anterior extension of the frontal bone and slightly beyond the posterior margin of the preorbital fossa. The anterior tip of the prefrontal extends between the dorsal and lateral flanks of the nasal bones. Further posteriorly, the prefrontal contacts the lacrimal (in lateral view) and the posteromedial process of the nasal (in dorsal view). The medial edges of the prefrontals are slightly concave and slightly tilted in relation to the midline of the skull.

The posterior region of the left prefrontal is unknown. However, the right prefrontal shows the base of a large stout prefrontal lateral process. On this side, the skull preserves the anterior border of the orbit, which is formed by the prefrontal and the lacrimal (Fig. 3A, B).

Nasal—The nasals are large, ‘Y’-shaped bones exposed on the dorsal surface of the skull (Figs. 2A, D, 3). The anterior process of the nasal is three times longer than the posteromedial process. The large anterior processes of both nasals meet medially, forming a long, triangular wedge that separates the maxillae along the midline. Each nasal has two posterior processes; the posteromedial one is elongated, separating the frontal and prefrontal bones and contributing to the skull roof.

In contrast, the posterolateral process of this bone is shorter, contacts the anterior edges of the prefrontal and the lacrimal, and forms the margin of the preorbital fossa.

Lacrimal—The right lacrimal is well preserved (Fig. 3). Its rectangular outline is exposed on the lateral surface of the skull and contributes to the anterior margin of the orbit. It articulates anteriorly with the nasal, exhibiting a rounded notch that forms the posterior part of the preorbital fossa. Its dorsal border forms a contact with the prefrontal. The lacrimal is tightly sutured to the dorsal surface of the maxilla. The anteroventral portion of the bone has a sharp anterior projection that surrounds the preorbital fossa laterally, and ventrally forms, together with the internal flange of the maxilla, the floor of this fossa, between the lacrimal and the nasal.

Jugal—Only the anterior part of the right jugal is preserved (Fig. 3). This small, stout, rectangular bone fragment is tilted upward and is laterally located between the maxilla and the lacrimal. Although this bone is placed near the preorbital fossa, it does not participate in the construction of the preorbital fenestrae.

Palatine—Both palatine bones are partially preserved (Fig. 4). The anterior tips of these bones connect with the maxillae ventrally, forming a ‘W’-shaped suture. Within this suture, each palatine possesses two long and sharp anterior processes. Laterally, the larger of these processes interlocks with a deep concavity of the maxilla, whereas the medial and smaller process meets with its opposite in the midline of the skull, forming a sharp triangle. The posterior surfaces of the palatines are

Metriorhynchidae

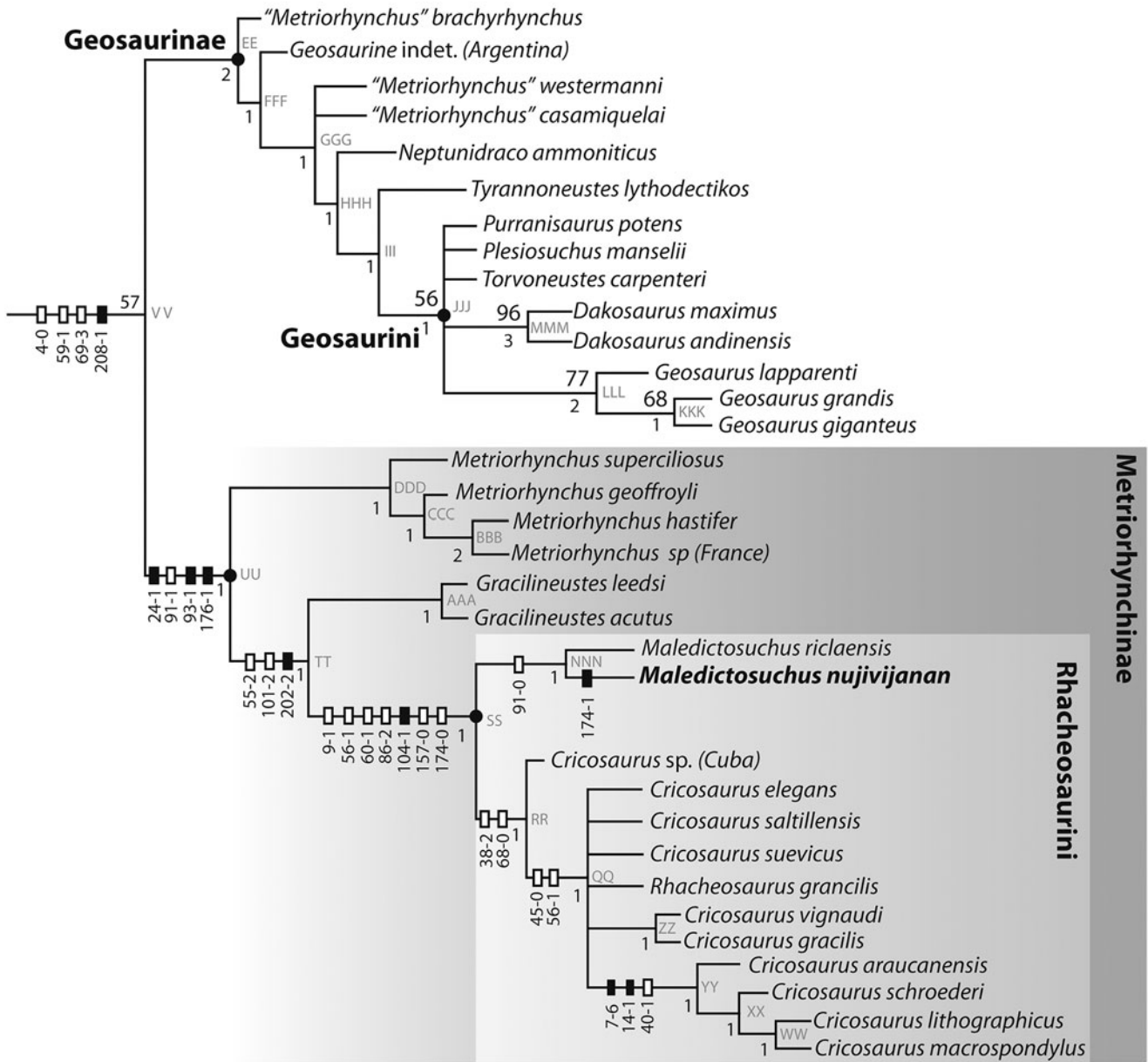


FIGURE 7. Strict consensus of 49 most parsimonious trees, showing the phylogenetic relationships of *Maledictosuchus nuyivijanan*, sp. nov., within Metriorhynchidae. The synapomorphies of different metriorhynchid taxa and the possible autapomorphy of *Maledictosuchus nuyivijanan*, sp. nov., are highlighted in black boxes. Numbers above branches represent the bootstrap values; numbers under lines represent the Bremer support values.

strongly eroded, leaving exposed the sediments that infill the nasopharyngeal ducts. The palatines extend inwardly into the skull in the posterior cross-section, forming the lateral external wall of the nasopharyngeal ducts.

Vomer—This bone is visible only in posterior cross-section (Fig. 2A, D), as a ‘Y’-shaped bone with the dorsal flanges enclosing the nasopharyngeal ducts and meeting ventrally with the palatines. The ventral component of this bone narrows at half its height.

Maxilla—Large parts of the maxillae are exposed along the ventral and dorsolateral surfaces (Figs. 2–5). The maxillae meet anteriorly along the dorsal skull midline, forming a

straight suture. These bones become progressively separated by the nasals towards their posterior ends. Laterally, the maxilla forms the anteroventral edge of the prefrontal fossa. On the lateral surface, the maxilla has a sharp posterior process that underlies the proximal end of the jugal bone. Although the posterior end of the left maxilla is badly preserved, the posterior tip of the maxilla extends posteriorly beyond the prefrontal fossa on the right side of the skull (in ventral and lateral views).

In ventral view, most of the midline suture of the maxillae is straight. There are low longitudinal ridges on the ventral surfaces of the maxillae, close to the snout midline. These ridges

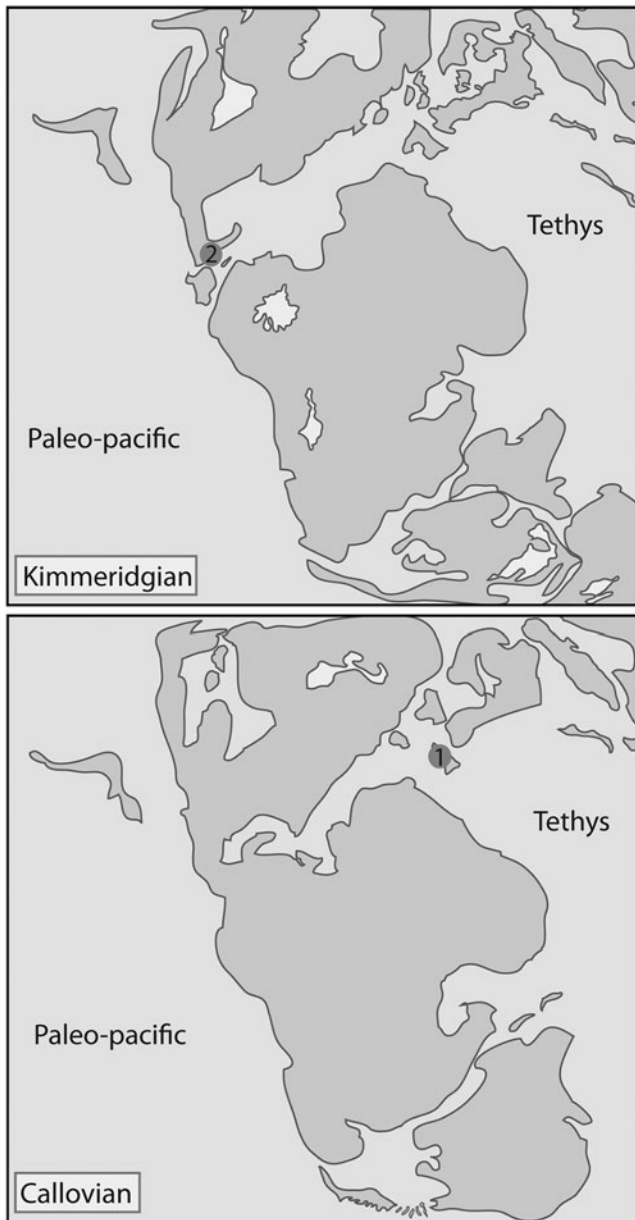


FIGURE 8. Distribution of the genus *Maledictosuchus* during the Late Jurassic. **1**, *Maledictosuchus riclaensi* (Ágreda Formation, Ricla, Zaragoza, Spain); **2**, *Maledictosuchus nuyivijanan*, sp. nov. (Sabinal Formation, near Tlaxiaco, Oaxaca, Mexico).

extend posteriorly beyond the ‘W’-shaped palatine-maxilla suture. Parallel to these ridges, each maxilla bears a shallow, elongated maxillopalatine groove. The tooth alveoli and the reception pits are aligned within a shallow alveolar groove.

Teeth—Each maxilla displays a row of curved, deeply rooted, slightly irregularly sized, and evenly spaced teeth. The teeth preserved in IGM 4863 include 10 teeth/alveoli in the right maxilla and 17 in the left one. The exposed alveoli are deep and extend for nearly the total depth of the maxilla. The alveolar outline is ovoid, approximately 8 mm long, and all alveoli are separated from each other by an interalveolar distance of approximately 4 mm. A row of small reception pits, positioned between the alveoli, is located slightly lateral to the alveolar row (Figs. 4, 5).

The tooth crowns are slightly curved backward and slightly compressed, particularly near their apex. The tooth widths at the bases of the crowns range between 4 and 5 mm, whereas their heights range between 15 and 20 mm. In cross-section (Figs. 5G, 6B), the teeth are almost oval. The crowns are conical and slightly longer than wide. The lingual edges are more curved than the labial ones.

All the crowns are carinated on both the anterior and posterior edges. The posterior and anterior carinae are tilted towards the labial and lingual extremes, respectively. Both carinae are smooth. Under scanning electron microscopy (SEM), the enamel on these cutting edges is evenly distributed and lacks serrations or undulations (Fig. 5B). The characteristics of these carinae match the non-zipodont condition described by Andrade et al. (2010) and Young et al. (2013c).

The enamel on both lingual and labial surfaces is distinctly ornamented (Fig. 5). The lingual surface is ornamented with conspicuous, narrow, and discontinuous ridges along two-thirds of the crown height. Smooth enamel is present on the apex of the lingual crown surface and on the entire labial crown surface.

DISCUSSION

Comparative Analysis

Specimen IGM 4863, the holotype and only known specimen of *Maledictosuchus nuyivijanan*, sp. nov., is herein identified as a metriorhynchoid crocodyliform because it possesses two diagnostic characters of this family described by Young et al. (2011). The first of these characters is related to the relative position of the prefrontal bones. In metriorhynchoids, the anterior edges of these bones are placed anterior to the orbits. The second relates to the position of the orbits. Although the orbits are extremely poorly preserved in IGM 4863, they must be positioned laterally and are anteriorly bordered by the prefrontals (Fig. 3).

Maledictosuchus nuyivijanan, sp. nov., displays a homoplastic character present in all metriorhynchids, bones of the rostrum lack or only have a weak ornamentation (Young et al., 2011) (character 4-0 in Phylogenetic Analysis and Supplementary Data 1 and 2). Within Metriorhynchidae, Geosaurinae and Metriorhynchinae differ in the shape of the palatine-maxilla suture. In geosaurines, such as *Purranisaurus potens* and *Dakosaurus andinensis*, the median suture between the palatines forms a single forward projection that separates the maxillae; by contrast, in metriorhynchines, such as *Cricosaurus araucanensis* and *C. lithographicus*, the maxillae separate the anterior ends of the palatines from one another. *Maledictosuchus nuyivijanan* is identified as belonging to the clade Metriorhynchinae because it shows the latter’s palatine-maxilla sutural pattern (Fig. 4). Additionally, *M. nuyivijanan* differs from species of *Metriorhynchus* von Meyer, 1830 (including the type species *M. geoffroyii* von Meyer, 1832, as well as *M. hastifer* (Eudes-Deslongchamps, 1868), and *M. superciliosus* (Blainville, 1853)) in the ornamentation of the frontal bone. In *Metriorhynchus*, this bone is ornamented with deep elliptical pits (Young et al., 2012), whereas in *M. nuyivijanan* this is practically smooth.

Parrilla-Bel et al. (2013:5, figs. 6–8, 14) identified four diagnostic autapomorphies of *Maledictosuchus*: the complex ‘W’-shaped palatine-maxilla suture; the exclusion of the jugal bone from the preorbital fenestra because the lacrimal and the maxilla are in contact; orbits longer than the supratemporal fenestrae; and reception pits that are located between the maxillary alveoli, offset slightly laterally on the anterior region of the maxillae and medially on the posterior region of the maxillae. Although the pattern of reception pits along the maxillae and dentaries is uncertain and the relative sizes of the orbit and

supratemporal fenestra are unknown in *M. nuyivijanan*, sp. nov., it is possible to conclude that this new species is unmistakably referable to the genus *Maledictosuchus* because it shows the first two of these autapomorphies.

The results of the phylogenetic analysis performed in this study show that *Maledictosuchus nuyivijanan*, sp. nov., is located within Metriorhynchinae, nested inside Rhacheosaurini as the sister taxon of *Maledictosuchus riclaensis* (Fig. 7). This new species shows distinctive dental characteristics among members of Rhacheosaurini, in that the teeth have cutting edges or carinae on the mesial and distal surfaces (bicarinated), whereas teeth without cutting edges are present in *Rhacheosaurus gracilis* and at least three species of *Cricosaurus* (i.e., *C. suevicus* [Fraas, 1901], *C. elegans* [Wagner, 1852], and *C. schroederi* Karl, Gröning, Brauckmann, and Knötschke, 2006). The new species also differs from both previously known Mexican species of Rhacheosaurini. In *Cricosaurus saltillensis*, the anterior margin of the jugal bone forms the lateral edge of the preorbital fossa and sutures with the maxilla, the anterior edge of the frontal bone has an irregular suture with the nasals, and the anterior process of the nasal is two times longer than its posteromedial process (Buchy et al., 2013). In contrast, in *M. nuyivijanan*, the jugal is excluded from the preorbital fossa, the suture between the frontal and nasal bones is straight, and the nasal bone has an anterior process that is three times longer than its posteromedial process.

Maledictosuchus nuyivijanan, sp. nov., also differs from *M. riclaensis* (Fig. 6). In *M. riclaensis*, the anterior frontal process is comparatively narrower, and so short that it terminates posterior to and far from the anterior margins of the prefrontal bones (Parrilla-Bel et al., 2013:fig. 10). In contrast, in *M. nuyivijanan*, the anterior frontal process is broad and occupies a large part of the skull roof, between the prefrontal bones; it is so long that it reaches the level of the anterior edges of the prefrontal bones. In addition, the teeth also have distinctive characters that distinguish these species. In *M. riclaensis*, all teeth are oval in cross-section, lack carinae, and the enamel on their lingual and labial crown surfaces is ornamented with apicobasally aligned ridges (due to the preservation, it is impossible to know if these ridges reach the apex; Parrilla-Bel et al., 2013:13, fig. 15) (Fig. 6C, D). In contrast, in *M. nuyivijanan*, all teeth are suboval in cross-section (the lingual surface of the crown is noticeably more curved than the labial one), are bicarinated, and the enamel is smooth on the labial crown surface and bears only some discontinuous subtle apicobasal ridges that are evenly distributed on the lingual surface (Fig. 6A, B) (see character 174-1 in Phylogenetic Analysis and Supplementary Data 1 and 2).

Phylogenetic Analysis

The cladistic analysis resulted in 45 most parsimonious trees of 668 steps, each with a consistency index of 0.484 and a retention index of 0.854. The topology obtained in the strict consensus (Fig. 7) resembles that recovered in previous analyses (e.g., Parrilla-Bel et al., 2013; Young et al., 2013c; Herrera et al., 2015); however, the inclusion of *Maledictosuchus nuyivijanan*, sp. nov., produced two small changes (Fig. S1 in Supplementary Data 2). In our results, ‘Metriorhynchidae indet. (Cuba)’ is positioned as the sister of Thalattosuchia and the topology among the most derived members of Rhacheosaurini is slightly different from that of previous hypotheses (Fig. S1 in Supplementary Data 2).

Metriorhynchidae is supported by the following characters (Fig. 7): humerus-antibrachium joint surface planar and limiting the possible motion (character 208-1); the rostrum bones (premaxilla and maxilla) are weakly ornamented with an

irregular pattern of ridges, rugosities, and anastomosing grooves (character 4-0); in dorsal view and between the supra-temporal fossa, the parietal width is greater than 75% of frontal width (character 59-1); and the orbit is positioned laterally (character 69-3). Due to the mode of preservation of IGM 4863, holotype of *Maledictosuchus nuyivijanan*, sp. nov., only two of these characters are preserved, supporting its inclusion within the family Metriorhynchidae (the weak superficial ornamentation of maxilla and the lateral position of the orbit; Figs. 2–4).

Our phylogenetic analysis supports the monophyly of the subfamily Metriorhynchinae, which is diagnosed by four characters (Fig. 7). The inclusion of IGM 4863 within this clade is justified because it shares one of these characters: the palatine anterior margin shows two lateral anterior processes (character 93-1). Because of its mode of preservation, this specimen cannot be assessed for the other two synapomorphies of the clade (the relative height of the lacrimal is less than 40% of the orbit height [character 24-1] and the hypocentrum of the atlas is short, subequal to odontoid process length, ca. 5% [character 176-1]). Results of our study reveal a homoplasy of Metriorhynchinae, in which the palatine lacks the midline anterior process (character 91-1); this character displays a remarkable alternative state that is shared by *Maledictosuchus riclaensis* and IGM 4863: the palatine has a well-developed midline anterior process (character 91-0).

In our phylogenetic hypothesis (Fig. 7), seven characters support the monophyly of Rhacheosaurini. These characters include the external nares bifurcated by a premaxillary septum (character 9-1); the angle between the medial and lateral posterior processes of the frontal is about 60–70° (character 56-2); the frontal-postorbital suture is lower than the intertemporal bar (character 60-1); in lateral view, the infratemporal fenestra (= laterotemporal fenestra) is shorter in length than the orbit (less than 25%) (character 86-2); the maxillary tooth crowns are weakly or not mediolaterally compressed (at the crown base the width is greater than 90% of the length) (character 157-0); macroscopic ornamentation of the tooth enamel is absent (under SEM view some ripples may be present) (character 174-0); and the occurrence of a paroccipital process oriented dorsolaterally at a 45° angle (character 104-1). The phylogenetic position of *Maledictosuchus nuyivijanan*, sp. nov., within this tribe is weakly supported because the fragmentary nature of IGM 4863 shows only one of these Rhacheosaurini characters: the maxillary teeth are only weakly or not mediolaterally compressed (Fig. 6B; character 157-0 in Fig. 7). By contrast, *M. nuyivijanan* clearly lacks one of these Rhacheosaurini characters: the tooth enamel is smooth or unornamented (character 174-0), whereas in *M. nuyivijanan* the tooth enamel is ornamented with ridges on the lingual crown surface (Fig. 6; character 174-1 in Fig. 7). Our results also suggest that the latter tooth-enamel character is an autapomorphy of *M. nuyivijanan*; however, this character has been observed in replacement teeth, but not in functional teeth of *M. riclaensis* (Parrilla-Bel et al., 2013:13). Therefore, additional material of *M. riclaensis* is required to conclude if ornamentation of tooth enamel represents another diagnostic character of the genus *Maledictosuchus*.

Our study shows two monophyletic subgroups within Rhacheosaurini: the *Cricosaurus* + *Rhacheosaurus* clade and the genus *Maledictosuchus*. In the framework of this analysis, IGM 4863 cannot be included within the clade of *Cricosaurus* + *Rhacheosaurus* because neither of the two diagnostic characters of this group (in dorsal view, the anterior margin of supra-temporal fossa reaches at least the postorbital [character 38-2] and the posterior margin of the parietal-squamosal is largely straight [character 68-1]) are preserved in

IGM 4863 (Fig. 7). In addition, the monophyly of *Maledictosuchus*, including *M. riclaensis* and *M. nuyivijanan*, sp. nov., is supported based on the occurrence of a unique character among metriorhynchids: the presence of a midline anterior process on each palatine (Fig. 4; character 91-0 in Fig. 7). The lateral anterior processes of these two bones are a synapomorphy of the subfamily Metriorhynchinae (character 93-1), that together with the midline anterior processes of the palatines that form a single acute median process forms a 'W'-shaped palatine-maxillae suture already described in both species (Fig. 4) Finally, the present study identifies a peculiar character present in *M. nuyivijanan*, sp. nov., that distinguishes it from *M. riclaensis*. This character is the presence of tooth enamel that is largely smooth but with short, well-spaced, and well-defined apicobasally aligned ridges on the basal half of the crown (Fig. 6B; character 174-1 in Fig. 7).

Biogeography of *Maledictosuchus*

The Late Triassic–Jurassic breakup of Pangea gave rise to two large landmasses that eventually separated into the modern continents: Laurasia in the north (comprising North America and Eurasia) and Gondwana in the south (including South America, India, Australia, Antarctica, and Africa). The separation of these landmasses provides the framework for a significant Jurassic biogeographic event. The intercontinental marine pathway created between Laurasia and Gondwana gradually became wider and deeper, allowing an open interchange of marine faunas between the eastern edge of Panthalassa and the western end of the Tethys Sea (Hsü and Bernolli, 1975; Westermann, 1993; Bartolini and Larson, 2001; Iturralde-Vinent, 2003). Although the development of this marine pathway has been treated as a single opening event, this was a result of four regional sea opening events that include: the Hispanic Corridor, developed between Europe, northwestern Africa, and eastern North America; the Caribbean Corridor, created between northern South America and the Yucatán block in southern North America (often, the term Caribbean Corridor is used as a synonym of the Hispanic Corridor; Arratia et al., 2004; Poyato-Ariza and Martín-Abad, 2016); the opening of the Gulf of Mexico; and the marine transgressions of Panthalassa into central Mexico (see Bartock, 1993; Alaníz-Alvarez et al., 1996).

The Jurassic marine intercontinental corridor between the Tethys and Panthalassa was an important paleogeographic element that impacted the composition and distribution of Jurassic and Cretaceous marine faunas. This corridor was a dispersal route for marine faunas. Its effects on the geographic distribution of some benthic invertebrates began in the Hettangian (Early Jurassic) (Sha, 2002; Hodges and Stanley, 2015); however, its influence on the distribution of pelagic invertebrates only becomes clear a little later, from the Pliensbachian (Early Jurassic) (Damborenea, 2000; Aberhan, 2001; Damborenea et al., 2013). This corridor also was a route of dispersal for pelagic reptiles from the Oxfordian (Late Jurassic) (Gasparini and Iturralde-Vinent, 2006; Bardet et al., 2014).

During the Jurassic, the Tlaxiaco Basin was a depocenter for continental and marine sediments generated by transgressions of the Panthalassa Ocean onto Mexico. During the Kimmeridgian, this basin was connected to the Tethys Sea via the Gulf of Mexico and the Hispanic Corridor. Thus, the marine fossils of the Tlaxiaco Basin represent an important record of the dispersal of marine faunas along the Hispanic Corridor. *Maledictosuchus nuyivijanan*, sp. nov., is the first Kimmeridgian record of *Maledictosuchus* in the Americas and the second species known of this genus (Fig. 8). Its temporal

and geographic positions contrast with those of *M. riclaensis*, collected from Callovian sediments of the Agreda Formation, near Ricla town, Zaragoza, Spain (Parrilla-Bel et al., 2013). Other metriorhynchids already known from the Hispanic Corridor area of America include the Oxfordian specimens of *Cricosaurus* sp. and indeterminate specimens from the Jagua Formation of Cuba (Gasparini and Iturralde-Vinent, 2006), as well as the Kimmeridgian–Tithonian remains of *Cricosaurus*, *Dakosaurus*, and *Torvoneustes* from Mexico already mentioned (Barrientos-Lara et al., 2016). Although *Cricosaurus* and *Dakosaurus* have a wide distribution, including localities outside of the Hispanic Corridor, in South America and Europe; the distribution of *Torvoneustes* and *Maledictosuchus* is restricted to the Tethys Sea domains in Europe and the Americas.

For a long time, the Mexican record of Jurassic marine vertebrates was poor and practically restricted to reptiles (see Buchy, 2007, 2008; Buchy et al., 2003, 2006, 2007, 2013; Cadena-Rangel, 2015); however, the discovery of the Llano Yosobé site is revealing a rich vertebrate assemblage showing affinities with the faunas from other regions. *Maledictosuchus nuyivijanan*, sp. nov., is added to the fossil assemblage of Llano Yosobé, in which the vertebrates constitute an unusual group that includes at least the following: (1) taxa that are shared between the western and eastern domains of the Tethys Sea such as the pliosaurid *Liopleurodon* Sauvage, 1873, the metriorhynchids *Torvoneustes* and *Maledictosuchus*, and the fish *Pleuropholis* Egerton, 1858 (Barrientos-Lara et al., 2016; Alvarado-Ortega and Brito, 2016); (2) a new species of *Notoemys* Cattoi and Freiburgh, 1961, a turtle that has a restricted distribution from the western domain of the Tethys (Cuba, Caribbean region) to the western coastal edges of South America (Colombia and Argentina) (López-Conde et al., 2017); and (3) relatives of taxa with a wider distribution, such as the hybodontid shark *Planohybodus* Rees and Underwood, 2008, abundant remains of osteichthyans belonging to the pycnodontiform *Gyrodon* Agassiz, 1833, and Lepisosteiformes, including *Nhanulepisosteus mexicanus* Brito, Alvarado-Ortega, and Meunier, 2017, and the remains of ichthyosaurs that may represent the family Ophthalmosauridae (Alvarado-Ortega et al., 2014).

CONCLUSIONS

Specimen IGM 4863, the holotype of *Maledictosuchus nuyivijanan*, sp. nov., displays the diagnostic character that supports its inclusion within the genus *Maledictosuchus*: the palatine-maxilla suture is 'W'-shaped. The new species differs from the type species of this genus, *M. riclaensis*, in the relative anterior extensions of the prefrontal and frontal bones, as well as in the dorsal shape of the frontal. In *M. riclaensis*, the frontal has a narrow anterior end that does not reach the anterior edge of the prefrontal bones; by contrast, in *M. nuyivijanan*, the anterior end of the frontal is wide, rounded, and reaches the anterior edges of the prefrontal bones. Additionally, teeth of *M. nuyivijanan* exhibit bicarinated crowns, a smooth labial surface, and a lingual surface ornamented with longitudinal ridges, whereas in *M. riclaensis*, the tooth crowns are uncarinated and both surfaces are covered with considerably more conspicuous ridges. This conclusion is also supported by the phylogenetic analysis performed in this research, in which *M. nuyivijanan* and *M. riclaensis* form a clade (Fig. 7).

The holotype of *Maledictosuchus nuyivijanan*, sp. nov., was collected in the Kimmeridgian marine sediments of the Llano Yosobé, a small outcrop of the Sabinal Formation located near the town of Tlaxiaco, Oaxaca, Mexico. Thus, this species is the

youngest representative of the genus so far known and the only one recovered from the Americas. This finding extends the geographic and spatial distribution of *Maledictosuchus* within the Tethys Sea domain, from the Callovian of Spain to the Kimmeridgian of Mexico. The presence of *M. nuyivijanan* in Tlaxiaco adds to the growing number of marine vertebrate taxa known from this site, which has an unusual taxonomic composition, including taxa previously known from other regions, such as the eastern domain of the Tethys Sea in Europe, the western part of the Tethys Sea in the Caribbean, and the western coastal region of South America.

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